

28. The Comparative Anatomy of the Tongues of the Mammalia.—IX. Edentata, Dermoptera, and Insectivora. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society and Demonstrator of Anatomy, University College.

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(Text-figures 50–57.)

CONTENTS.

	Page
Order Edentata	515
„ Dermoptera	522
„ Insectivora	523
Conclusions	527
Bibliography	527

Order EDENTATA.

The tongues of the Edentata are characterised by a high degree of specialisation of their extrinsic muscles, and by a slight or moderate development of their glands and gustatory organs. Their mobility is greater than that of all other Mammalian tongues except those of *Zaglossus* and *Acanthoglossus*. In the Myrmecophagidæ and Manidæ the mobility is designed mainly for the purposes of prehension; but in other Edentates prehension is combined with a mechanical action of the food.

Form, Apex and Lateral Borders:—The tongue is long, vermiform and not flattened anteriorly in the Myrmecophagidæ (text-fig. 50); it is cylindrical posteriorly and flattened anteriorly in the Manidæ (text-fig. 52); it is long, flat and triangular in the Dasypodidæ and *Orycteropus* (text-fig. 52); and it is short, with the usual Mammalian form in the Bradypodidæ*.

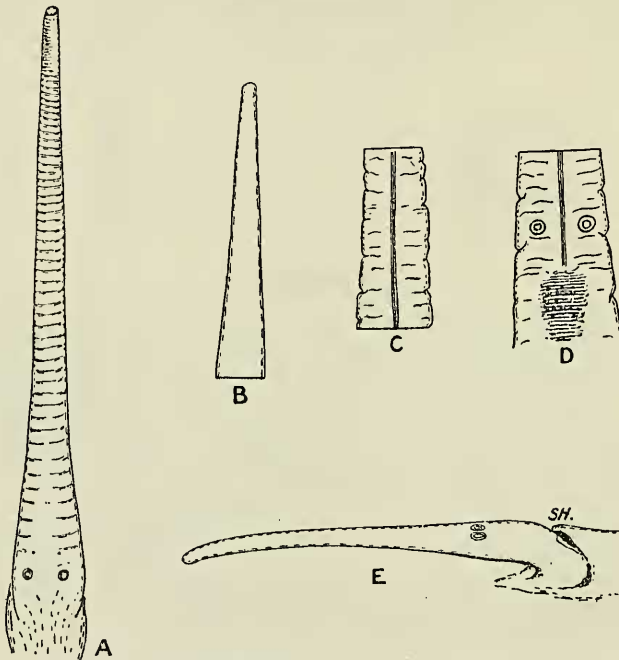
The apex is rounded in the Bradypodidæ; it is pointed in *Orycteropus*; and it bears peculiar globular or pointed organs in the other Edentates. These take the form of globular expansions of the whole apex in the Myrmecophagidæ and Dasypodidæ, or of a button-like structure attached to the centre of the apex in the Manidæ (text-figs. 50 and 52). No trace of this terminal swelling is present in the Bradypodidæ and *Orycteropus*. I was unable to examine the swellings microscopically to settle their nature, as the tongues are preserved in the Museum of the Royal College of Surgeons. Some authors regard them as sense organs, and Mayer (14) described the swelling in *Myrmecophaga* as gustatory in function. Perhaps

* See text-fig. 10 in my paper on the anatomy of *Bradypus* (26).

they are allied to the marginal lobes in *Galeopithecus*, the Pinnipedia and Cetacea.

Mayer (14) described two small sharp processes, with their ends directed forwards and inwards, beneath the apex of the tongue of *Dasypus peba*, *D. decem-*, *D. novem-*, and *D. octocinctus*. They receive prolongations of the lingual musculature. Their function is probably to capture and grip food, and Mayer thought they might open and close and be useful for killing insects.

Text-figure 50.



The tongues of the Myrmecophagidæ. A: *Tamandua tetradactyla*; B.C.D: the front, middle, and back of the dorsum in *Myrmecophaga jubata*; E: side view of the tongue in *Myrmecophaga* showing the sheath (SH.) for the tongue.

The lateral borders are not distinguishable on those tongues which are cylindrical throughout (*Myrmecophaga*, *Tamandua*, *Cyclothurus*). In *Manis* the flattened anterior part has a pronounced edge, but the posterior cylindrical part has no distinct edge. In the Dasypodidæ and *Orycteropus* the lateral borders are pronounced and moderately thick, but the Brady-podidæ have borders of considerable vertical depth. Lateral organs are only found in some specimens of *Dasypus*.

Sulci and Ridges:—Median dorsal sulci are found in *Manis*,

Myrmecophaga and *Orycteropus*. In *Manis* (text-fig. 52) there is a wide, shallow groove on the flattened anterior part of the tongue. In *Orycteropus* (text-fig. 52) a fine groove runs along the greater part of the dorsum. And in *Myrmecophaga* (text-fig. 50) there is a shallow groove behind the circumvallate papillæ; when it is traced forwards it merges into a central strip of the tongue in which the mucosa is thrown into transverse folds. Numerous fine transverse sulci are found in these animals and in *Tamandua* and *Cyclothurus*.

Median ridges are present on the inferior surface of the tongue in *Orycteropus* and *Tatusia*. In the former (text-fig. 52) there are three ridges and many transverse sulci; in the latter there is a single ridge.

In the case of Edentates with long, vermiform, protrusible tongues there are sheaths into which they can be retracted. In text-fig. 52 is shown a corrugated cuff-like sheath in *Manis*.

Circumvallate Papillæ:—The following list summarises the observations made by myself and those recorded by others:—

Family MYRMECOPHAGIDÆ.

- Myrmecophaga jubata*: 2 vallate papillæ (Flower, 8; and self).
 „ *didactyla*: 2 vallate papillæ (Carus and Otto, 4).
Tamandua tetradactyla: 2 vallate papillæ (Mayer, 14; Münch, 16)
Cyclothurus: 2 vallate papillæ.

Family DASYPODIDÆ.

Podwisotzky (19) showed how all species have two vallate papillæ, and this has been confirmed by observations of many authors on all known species of *Dasypus*, *Tatusia* and *Tolypeutes*. The records have been collected by Oppel (17).

Family BRADYPODIDÆ.

- Bradypus tridactylus*: 2 vallate papillæ (Cuvier, 6; Sonntag, 25).
 „ „ : 3 vallate papillæ (Mayer, 14).
 „ „ : 2 vallate papillæ (Mayer, 14).
 „ *cuculliger*: 2 vallate papillæ (Brücher, 2).
Choloepus didactylus: 2 vallate papillæ.
Chlamyphorus truncatus: 2 vallate papillæ (Tuckerman, 21).

Family MANIDÆ.

- Manis pentadactyla*: 3 vallate papillæ in a triangle (Carus and Otto, 4).
 „ *tetradactyla*: 3 vallate papillæ in a triangle (Mayer, 14).
 „ „ : 2 vallate papillæ (Carus and Otto, 4).
 „ *javanica*: 3 vallate papillæ in a triangle.
 „ „ : 3 vallate papillæ in a triangle (Oppel).

Family ORYCTEROPODIDÆ.

Orycteropus capensis: 3 vallate papillæ in a triangle.
 „ „ : 3 vallate papillæ (Rapp, 20).

It is thus evident that with very few exceptions the American Edentates have a pair of circumvallate papillæ, whereas the African forms have three papillæ disposed in a triangle with the apex directed backwards.

The papillæ are frequently found retracted within a deep fossa, but those in some of the Dasypodidæ stand up very prominently. In the specimen of *Tatusia* shown in text-fig. 51 they are very prominent, and it is at first sight difficult to distinguish them from the larger fungiform papillæ on the posterior part of the oral division of the dorsum.

The vallate papillæ are close to the epiglottis in the Bradypodidæ, Dasypodidæ, Myrmecophagidæ and *Orycteropus*, but they lie far from it in *Manis*, thus making the basal part of the tongue long.

In *Tamandua* (text-fig. 50) there are two small pin-hole-like pits in front of the vallate papillæ, but I was unable to make a histological examination to ascertain whether or not they receive the secretions of glands.

The vallate papillæ are circular on plan, and cylindrical or conical on elevation, with the apex of the cone attached to the tongue. The surface is smooth or granular, and a histological examination shows that the granular effect is produced by several secondary papillæ. The fossa is well marked, and the vallum frequently overlaps the edge of the papillæ. Oppel (17) has published an illustration of a section through a papilla in *Manis javanica*, showing how the long axes of the taste-buds run downwards and outwards towards the fossa which passes under the base of the cone-like papillæ.

Tuckerman (21) pointed out that the papillæ in *Dasyppus peba* resemble those of the higher Mammalia, but those of *Chlamydomorphus truncatus* are very similar to those of the Marsupialia; their resemblance to the anterior papillæ in *Belideus* and *Phalangista* is very marked indeed.

Fungiform Papillæ:—I did not observe any trace of fungiform papillæ in *Myrmecophaga*, *Tamandua*, *Cyclothurus* or *Manis*, nor has any other anatomist described them. They are present in all other Edentata, but they are never very numerous. No apical cluster exists, but they have the usual arrangement in rows of varying degrees of obliquity behind that in the Dasypodidæ; and they stretch right across the dorsum (text-fig. 51). In the Bradypodidæ* the apical cluster varies in size, but the papillæ do not cross the middle line. In *Orycteropus* there is no apical cluster, and the papillæ only form a dorsal bounding zone. Tuckerman (21) points out that some of the papillæ are sunk in

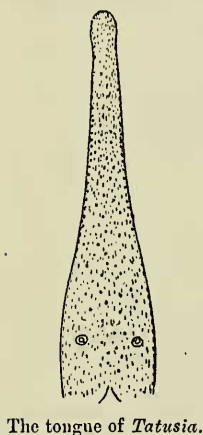
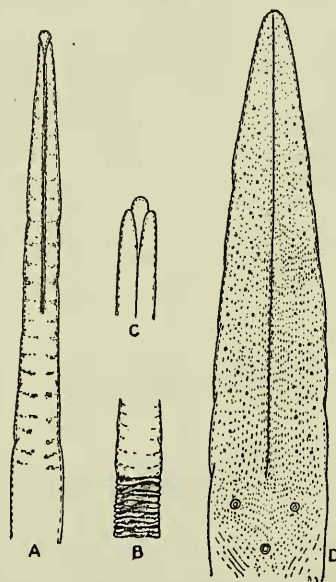
* See foot-note on page 515.

little hollows in *Dasypus peba*; and those lying on the posterior part of the tongue have well-developed taste-buds. No papillæ fungiformes are present on the lateral borders.

Lateral Organs:—There appears to be considerable variation in the lateral organs, for the views of various authors are conflicting. I observed no trace of organs in *Myrmecophaga jubata*, *Tamandua tetradactyla*, *Cyclothurus didactylus*, *Manis* (sp. ?), *Orycteropus capensis*, *Bradypus tridactylus*, *Tatusia* (sp. ?) and *Dasypus villosus*. Mayer (14) observed them in *Myrmecophaga* and the *Dasypodidæ*. Boulart (1) and Tuckerman (21)

Text-figure 52.

Text-figure 51.

The tongue of *Tatusia*.

The tongues of the *Mandæ*. A.B: front and back of the tongue of *Manis*; C: under surface of the apex of the tongue of *Manis*; D: the tongue of *Orycteropus capensis*.

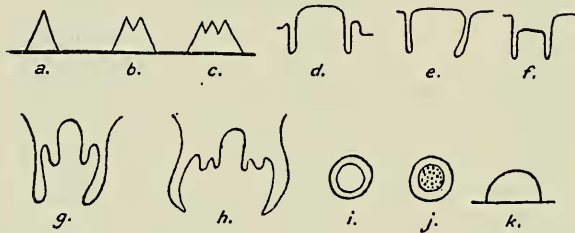
found them in *Tatusia*, and the latter author found them taking the form of minute openings in several Armadillos; taste-buds and serous glands were connected to them. Gmelin (9) found no trace of organs in *Orycteropus*, the Armadillos and Sloths, and Podvisotzky (19) saw them in *Dasypus sexcinctus*. So it is evident that the organs are variable in the *Dasypodidæ*, but usually absent in the other *Edentates*.

Conical Papillæ:—These papillæ are well-marked in the *Bradypodidæ*, *Dasypodidæ* and *Orycteropus*, but I found no trace of them on naked-eye examination in the *Myrmecophagidæ* or

Manis. In the species in which I observed them they have the usual arrangement in an apical cluster, and in rows of varying degrees of obliquity behind that. They are also present on the lateral borders, but they are restricted to a narrow bounding zone on the inferior surface of the tongue. They stretch back to the neighbourhood of the epiglottis, but those on the base of the tongue are not very large. In *Orycteropus* (text-fig. 52) the individual papillæ are easily distinguished; in the Bradypodidæ they can only be detected through a lens; and in the Dasypodidæ they vary in prominence to such a degree that the dorsum appears granular (*Dasypus*) or almost shaggy (*Tatusia*). Some of the types of conical papillæ in the Dasypodidæ and Bradypodidæ are shown in text-fig. 53.

Oppel (17) described scanty conical papillæ in *Manis*, and Tuckerman (21) stated that those in *Dasypus villosus* are intermediate in character between the coronate and fasciculate papillæ in Marsupials and the mechanical papillæ in higher Mammalia. Secondary papillæ are found on many of the main ones.

Text-figure 53.



The papillæ in the Edentata. *a-c*: conical papillæ; *d-h*: circumvallate papillæ cut vertically; *i-k*: fungiform papilla.

Glands.—Oppel (17) and Podwisotzky (19) mapped out the serous and mucous glands of the tongue in *Manis javanica*. They showed that the mucous glands form a cluster on the base of the tongue, whilst the patch of serous glands lies far forwards round the vallate papillæ. Owing to the large size of the salivary glands the mucous glands are not very numerous. I did not observe any patulous glandular orifices in the Myrmecophagidæ or Orycteropodidæ. In the specimen of *Manis* at my disposal the base of the tongue was concealed to a considerable extent by the sheath. But in *Bradypus* I observed a number of orifices and lymphoid nodules. No apical gland of Nuhn is present.

The serous glands vary in the Dasypodidæ; they are numerous in *Dasypus villosus*, but scanty in *D. peba*.

Lytta.—The only Edentates which possess a lytta are *Manis gigas* and *M. javanica*. It has been described and figured by Oppel (17) and Rapp (20); and Mayer (14) points out that it is

large as in many Carnivora. I was unable to cut into the tongues of *Manis*, *Myrmecophaga* or *Orycteropus*, but I found no trace of it in *Tamandua*, *Bradypus*, *Dasypus* or *Tatusia*.

The *frenum* is short in all Edentates.

There is no trace of *plicæ fimbriatæ* or *frenal lamellæ*. The musculature and elastic tissue have already been fully described by Owen (18) and others. No intermolar eminence is present.

Sir William Flower (27) came to the following conclusions as regards the affinities of the Edentates:—"All the American Edentates at present known, however diversified in form and habits, belong to a common stock. The *Bradypodidæ*, *Megatheridæ*, and *Myrmecophagidæ* are closely allied, the modifications seen in existing families relating to food and manner of life. The ancestral forms may have been omnivorous, like the present Armadillos, and gradually separated into the purely vegetable and purely animal feeders; from the former are developed the modern Sloths, from the latter the Anteaters. The Armadillos are another modification of the same type, retaining some more generalised features, as those of the alimentary organs, but in other respects, as their defensive armature, remarkably specialised.

"The two Old-World forms *Manidæ* and *Orycteropidæ* are so essentially distinct from all the American families, that it may even be considered doubtful whether they are derived from the same primary branch of mammals, or whether they may not be offshoots from some other branch, the remaining members of which have been lost to knowledge."

It was shown above that the tongues of the American Edentates have two circumvallate papillæ, whereas those of the Old-World forms have three; and it is only in rare specimens that this arrangement is departed from.

If the Armadillos were like the ancestral forms, as Flower believed them to be, it is necessary to see whether their tongues could have been transformed into those of the *Myrmecophagidæ* and *Bradypodidæ*. The tongue of any Armadillo is long and triangular, with a slightly bulbous apex and a good supply of fungiform and conical papillæ; and in some species there are lateral organs. If the tongue be simply shortened, with loss by absorption of the apical swelling, it would become indistinguishable from that of *Bradypus*. Conversely, enormous elongation of the tongue, with retention and specialisation of the apical swelling, produces a tongue like that of *Tamandua* or *Myrmecophaga*; and as the tongue in these insectivorous animals is merely a glutinous finger, the conical and fungiform papillæ on the dorsum would undergo disuse atrophy. So it is evident that the mere changes in form, with or without disuse atrophy, would convert the tongue of an Armadillo into that of a Sloth or an Anteater.

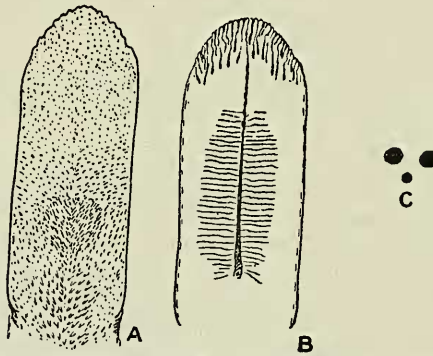
The tongue of *Manis* resembles those of the *Myrmecophagidæ* in its general form, and in the specialisation of the apex to form a sensory organ; but the likeness between them stops there.

These resemblances are the result of convergence and are, consequently, no test of affinity. There is, moreover, no resemblance between the tongues of *Manis* and *Orycteropus*, beyond the characters of the circumvallate papillæ. If they have arisen from a common form, the great contrast between them is the result of adaptation to a particular diet and mode of feeding. And there appears to be no affinity between the tongues of the African and American Edentates. So it is evident that the characters of the tongues lend additional support to Flower's views on the mutual affinities of the Edentata.

Order DERMOPTERA.

The tongue of *Galeopithecus volans* (text-fig. 54) is long, narrow and thick, and its free part is of considerable extent. The upper surface is chocolate-coloured, but the lower surface is pale. The *apex* is rounded, devoid of a notch, and divided into lobules by fissures, which pass backwards and inwards for a considerable distance on the inferior surface. The *lateral borders* are full and rounded, and have well-marked lateral organs at their posterior extremities. A well-marked *median dorsal sulcus* runs back along the greater part of the oral division of the

Text-figure 54.



The tongue of *Galeopithecus volans*. A : dorsum ; B : under surface ;
C : vallate papillæ of a second specimen.

dorsum, but no transverse fissures diverge from it. The *median ventral sulcus* is equally well-marked, and transverse sulci diverge from its posterior part. There is no trace of a foramen cæcum or plicæ fimbriatæ, and the frenum is very short. No frenal lamella is present.

Papillæ:—The whole of the dorsum from the apex back to the epiglottis is covered with thickly-set, sharp, hard conical papillæ which have the usual arrangement in clusters and rows; and they increase in size from within outwards, and from before

backwards. They also cover the upper part of the lateral borders, but they are not present on the inferior surface of the tongue. They are of a simple character. In one tongue I was unable to detect any circumvallate or fungiform papillæ; but these were probably buried under the conical papillæ. In a second tongue the conical papillæ were short, the fungiform papillæ were scanty, but had the usual arrangement; and there were two large vallate papillæ, with a minute one in between.

Lateral Organs:—Owing to the great length of the oral part of the tongue, the lateral organs appear to be placed far back on the lateral borders. They are as well marked as those in Primates: and each consists of eleven laminae separated by deep sulci.

Sublingua:—Gregory (10) pointed out the *Galeopithecus* has a sublingua similar to that in *Tupaia*, but I was unable to detect either a sublingua or plicæ fimbriatæ in three tongues.

No lytta is present, and no gland orifices are visible on the base of the tongue.

Order INSECTIVORA.

The tongue, like other anatomical characters, is very simple in the Insectivora, and it is possible to show how the tongues of animals belonging to other Orders can be derived from them by specialisation of certain structures or areas. In the present paper the structural characters alone are dealt with, the phylogenetic considerations being postponed till all the systematic papers of this series have been completed.

The tongue is long and narrow in all species, and its free part is of considerable length. It usually thickens gradually from before backwards; but its thickness is not greater in proportion to its length in *Erinaceus* (text-fig. 55). The oral part of the dorsum is long, and the pharyngeal part is short in all species. The apex is rounded, truncated or pointed, and is usually devoid of a notch. The lateral borders are rounded, but they only possess lateral organs in *Erinaceus*.

Median dorsal sulci are absent, but transverse ridges and sulci may be produced by the impression of the palatal rugæ on the tongue. Median ventral sulci are absent, but median ventral crests are present in *Talpa* (text-fig. 56) and *Rhynchocyon* (text-fig. 57); they are blunt in the former, and sharp in the latter.

Circumvallate Papillæ:—In the Insectivora there are two large papillæ, or three papillæ in a triangle with the apex turned backwards. And the following list contains the observations of myself and others:—

Family Erinaceidæ:—Two papillæ in *Gymnura rafflesii*.

Three papillæ in all species of *Erinaceus*.

Family Centetidæ:—Three papillæ in *Centetes*, *Ericulus* and *Microgale*.

Family Solenodontidæ:—Three papillæ in *Solenodon paradoxurus*.

Family Potamogalidæ:—Three papillæ in *Potamogale velox*.

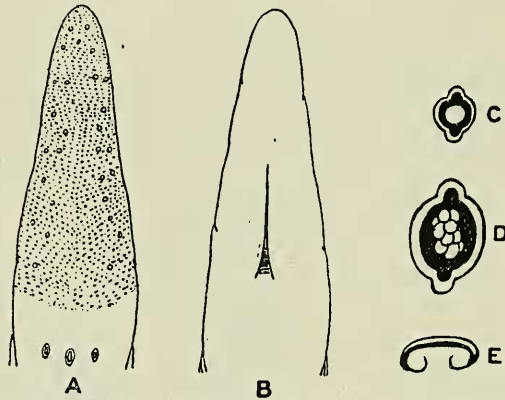
Family Chrysochloridæ:—Three papillæ in all species of *Chrysochloris*.

Family Talpidæ:—Two papillæ in all species of *Talpa*, *Myogale*, *Condylura*, *Scapanus* and *Scalops*.

Family Soricidæ:—Two papillæ in all species of *Sorex*.
Three papillæ in *Rhynchocyon*.

The papillæ are round or oval on plan, and cylindrical or conical on elevation. The surface is smooth or granular, and there may be a small central depression. The fossa and vallum are well-marked. Carrier (3) showed that the papillæ in *Erinaceus europæus* contain serous glands and ganglion cells, and their connective-tissue cores are very cellular. The ducts of these serous glands open along with those of the serous glands within

Text-figure 55.



The tongue of *Erinaceus europæus*. A: dorsum; B: under surface;
C-E: vallate papillæ.

the base of the tongue. The only other Mammals, so far as I am aware, in which there are glands within the vallate papillæ are the Chiroptera.

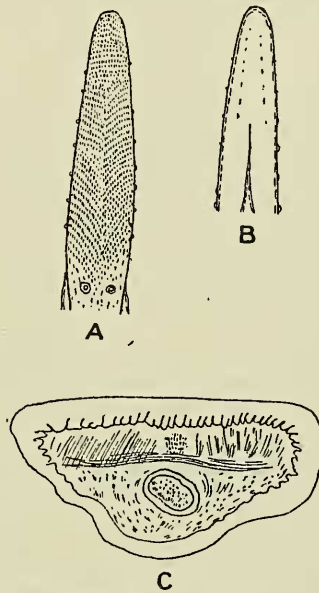
Fungiform Papillæ:—These papillæ are never very numerous, but more are present in *Erinaceus* and *Chrysochloris* (text-fig. 55) than in any other genus. It may be difficult to detect them, for they are usually very small. Dobson (7) points out, however, that they are prominent in *Gymnura rafflesii* and *Chrysochloris villosa*. They may be composed entirely of epithelial cells, as in *Erinaceus*, or they consist of both epithelial and connective-tissue elements.

Conical Papillæ:—In all species the conical papillæ are numerous and closely packed. They are usually very small on the oral part of the dorsum; and they are usually small on the

base as well. The basal papillæ are large in *Centetes* and *Chrysochloris*.

When examined through a hand lens they are seen to be simple in character, having one, two or three points. In *Chrysochloris* scoop-shaped forms are present. In many species they are composed entirely of epithelium, which is strongly cornified, the component cells being formed of the strata from the surface down to the Malpighian layer. The different forms are met with in genera of the same family; thus *Gymnura* has bifid papillæ, but *Erinaceus* has them divided into three points. So it is evident that the forms are simpler than in animals belonging to all the Orders hitherto considered in this series of papers.

Text-figure 56.



The tongue of *Talpa europæa*. A: dorsum; B: under surface;
C: cross-section showing the oval lytta.

Lateral Organs.—Many authors have described the lateral organs in *Erinaceus*, and some have stated that these structures are absent in all other genera. With both these remarks I am thoroughly in accord.

In *Erinaceus europæus*, according to Mayer (14) and Gmelin (9), the organ consists of two large folds well provided with taste-buds and fat. In the animal examined by myself (text-fig. 55) the organ varied on both sides. On the right side a fissure, with slightly curved ends, much as in *Hydrochærus capybara*; on the

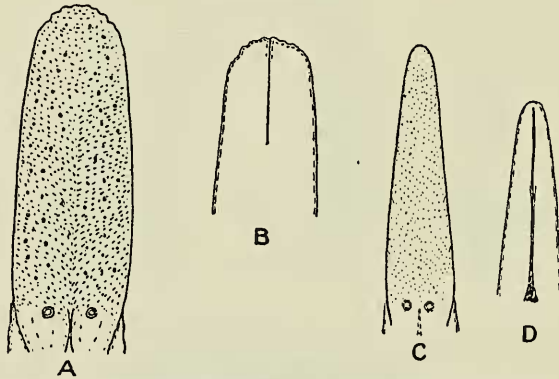
left side the fissure undercut part of the dorsum, thereby producing an overhanging lobe.

Glands:—I agree with Carlier (3), Oppel (17) and Podwisotzky (19) that the serous glands are very highly developed, and the mucous glands are scanty in *Erinaceus*. As was mentioned above, serous glands are present even within the vallate papillæ in *E. europæus*. No apical gland of Nuhn exists in any Insectivore.

The *frenum lingue* is short in all Insectivora except *Tupaia*. And it is fine in *Erinaceus*, but thick in *Talpa*, *Rhynchocyon*, etc. In no case is there any trace of frenal lamellæ as in the Lemuroid Primates.

Sublingua:—It has been shown by Owen (18) and Garrod that there is a sublingua in *Tupaia*; Owen described it as a fimbriate plica, but Garrod described it as resembling that in *Chiromys*. Vogt and Yung (24) recorded the presence of a sublingua in

Text-figure 57.



The tongues of *Chrysochloris trevelyani* (A and B) and *Rhynchocyon* (C and D).

In both cases a third papilla is concealed in the linear groove on the back of the dorsum.

some Insectivora. I found no trace of the sublingua in *Erinaceus*, *Centeles* and *Chrysochloris*, but it may be represented by the median ventral ridge in *Talpa* and *Rhynchocyon*. That ridge may correspond to the median crest which is found on the ventral surface of the sublingua in the Marsupialia and Primates. In that case the remainder of this organ has been absorbed into the tongue.

Lytta:—It has been shown by Nussbaum (28), Oppel (17), Hesse (11), and Ludwig Ferdinand, Prince of Bavaria (13), that the lytta is well-developed in *Erinaceus europæus*, *Sorex fodiens* and *Talpa europæa*. It is composed of muscle fibres, fat and fibrillar connective tissue, but no cartilaginous elements are present. The histological details are given fully in the papers enumerated above. I observed a very pronounced lytta in

Rhynchocyon. The lytta in the Insectivora is in many ways similar to that in the Lemuroid Primates.

Musculature:—This has been fully described by Carlier (3) and Oppel (17).

CONCLUSIONS.

1. The tongues of the Edentata and Insectivora are of particular interest, for they afford clear illustrations of some of the principles which should guide us in settling the blood-relationships of animals. Thus they exhibit primitive, convergent and adaptive characters.

2. The tongues of all the American Edentata can be derived from Armadillo-like forms.

3. The tongues of the Myrmecophagidæ are similar in many ways to that of *Manis*, but the resemblances have been produced by convergence.

4. All American Edentata have two circumvallate papillæ, but the African forms have three in a triangle.

5. The differences between the tongues of *Manis* and *Orycteropus* are the result of adaptive modifications.

6. It is a well-established principle of phylogeny that observations should be drawn from all parts of the body; and conclusions as to affinities should not be based on the examination of a single organ. The truth of this can be seen in a study of the Edentata; for an examination of the tongue alone would make one agree that *Manis* and the Myrmecophagidæ are closely related; an examination of the entire anatomy of these animals shows that that is not true.

7. The tongues of the Edentata are more mobile than those of all other Mammals except *Acanthoglossus* and *Zaglossus*.

8. The tongue of *Galeopithecus* has affinities with those of the Insectivora. The characters of its apex, however, are unique.

9. The tongues of the Insectivora are very primitive, for their mechanical papillæ are simple, their gustatory papillæ are not numerous and they have traces or complete examples of the lytta and sublingua. Many of their characters are similar to those of the Lemuroid Primates.

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